

A PHYLOGENETIC ANALYSIS OF THE *LAURENCIA* COMPLEX (RHODOMELACEAE) OF THE RED ALGAE

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This paper is dedicated to Prof. Dr F. Ardré
but it was not possible to include it in issues 2 & 3 of Vol. 18

ABSTRACT — A phylogenetic analysis of 29 species from the *Laurencia* complex was carried out based on 36 morphological and developmental characters. Taxa included nine species of subgenus *Laurencia*, 12 species of subgenus *Chondrophycus* and eight species of *Osmundea*. *Chondria* was the outgroup. Characters were associated with ecology (1 character), vegetative features (17 characters), male reproduction (8 characters), female reproduction and carposporophytes (3 characters) and tetrasporangia (7 characters). Twelve most parsimonious trees were produced with treelength of 148. Three large clades were resolved that corresponded to *Osmundea*, *Laurencia* subgenus *Laurencia* and *Laurencia* subgenus *Chondrophycus*. Subgenus *Chondrophycus* was resolved as the sister group of *Osmundea*. The position of *L. translucida* Fujii & Cordeiro-Marino is problematic, but it is probably allied to *Chondrophycus*. *Chondrophycus* is raised to generic rank and 12 new combinations in *Chondrophycus* are proposed.

RÉSUMÉ — Une analyse phylogénétique de 29 espèces du complexe *Laurencia* a été réalisée, sur la base de 36 caractères morphologiques et du développement. Les taxons comprennent neuf espèces du sous-genre *Laurencia*, 12 du sous-genre *Chondrophycus* et huit du genre *Osmundea*. *Chondria* a été choisi comme groupe extérieur. Les caractères sont relatifs à l'écologie (1 caractère), à des caractéristiques végétatives (17 caractères), à l'appareil reproducteur mâle (8 caractères), à l'appareil reproducteur femelle et aux carposporophytes (3 caractères), et aux tétrasporocystes (7 caractères). Douze arbres les plus parcimonieux de 148 pas ont été obtenus. Trois grands clades ont été résolus : ils correspondent au genre *Osmundea*, au sous-genre *Laurencia* et au sous-genre *Chondrophycus* du genre *Laurencia*. Le sous-genre *Chondrophycus* apparaît comme le groupe frère du genre *Laurencia*. *Chondrophycus* est élevé au rang de genre et 12 nouvelles combinaisons sont proposées dans le genre *Chondrophycus*. (Traduit par la Rédaction)

KEY WORDS: *Chondrophycus*, *Laurencia*, marine algae, *Osmundea*, Rhodomelaceae, Rhodophyta, taxonomy, cladistic analysis.

INTRODUCTION

With about 150 species, the *Laurencia* complex of the Rhodomelaceae is one of the most diverse and widespread assemblages of red algae (McDermid, 1988). In recent years there has been considerable interest in the taxonomy of the group and numerous new species have been described from around the world (e.g., *L. minuta* Vandermeulen *et al.*, 1990; *L. iridescens* Wynne & Ballantine, 1991; *L. verlaquei* Cormaci *et al.*, 1994; *L. kangjaewonii* Nam & Sohn, 1994; *L. maris-rubri* Nam & Saito, 1995). In addition, there has been considerable interest in the infrageneric classification of the assemblage. Early systematic work was summarized by McDermid (1988) and she outlined seven sections in two subgenera (*Laurencia* and *Chondrophyceus* Tokida & Saito *in Saito*) and a "*Spectabilis*" group. More recently, several new (or revised) taxa have been described including the section *Articulatae* (Zhang & Xia, 1985), the genus *Osmundea* Stackhouse (Nam *et al.*, 1994), the subgenus *Saitoa* (Furnari & Serio, 1993a), the section *Pelagosae* (Furnari & Serio, 1993b), and a "*Platycephala*" group (Gil-Rodriguez & Haroun, 1993). All of these taxonomic groupings have been proposed based on traditional morphological analyses and subjective assessments of relationships.

In this paper we carry out a cladistic analysis of the *Laurencia* complex as a means of evaluating various taxonomic proposals for the assemblage. Using phylogenetic systematics (*i.e.*, cladistics) we focus on the segregation of *Osmundea* (Nam *et al.*, 1994), and the potential distinction of *Laurencia* subgenus *Laurencia* and *Laurencia* subgenus *Chondrophyceus* at generic rank. In order to provide a rigorous evaluation of potential generic segregates within the complex, we include a number of species in the analysis that were described as potential intermediates between more clearly defined assemblages: *L. kangjaewonii* Nam & Sohn (1994), *L. gemmifera* Harvey (Fujii *et al.*, 1996), *L. translucida* Fujii & Cordeiro-Marino (1996).

MATERIALS AND METHODS

The 29 species of the *Laurencia* complex used in the study (Table 1) were selected because they represented the wide range of infrageneric taxa previously described for *Laurencia*, and because features of vegetative and reproductive morphology were well described for most taxa. In addition, the type species for most primary segregates at the generic, subgeneric and sectional levels (Table 1) were included. *Chondria* C. Agardh [based on *C. dasyphylla* (Woodward) C. Agardh and *C. tenuissima* (Goodenough & Woodward) C. Agardh] as characterized by Gordon-Mills (1987) was used as the outgroup. The characters and their character states (Table 2) were defined based on a literature investigation (Table 1). Several other characters such as colour and the presence or absence of lenticular thickenings were included in early analyses; however, consistency values were extremely low (*ca* 0.1), and these characters were omitted from subsequent analyses.

Table 1. Algae used in this study and sources of information.

Algae and authorities	Selected References
<i>Chondria</i> C. Agardh	Gordon-Mills, 1987; Gordon-Mills & Womersley, 1987
<i>Laurencia capituliformis</i> Yamada	Saito, 1967; Nam & Saito, 1995
^o <i>L. cartilaginea</i> Yamada	Nam & Saito, 1990; Nam & Sohn, 1994; Saito, 1967
<i>L. composita</i> Yamada	Masuda <i>et al.</i> , 1996
<i>L. crustiformans</i> McDermid	McDermid, 1989
<i>L. gemmifera</i> Harvey	Fujii <i>et al.</i> , 1996
<i>L. intermedia</i> Yamada	Saito, 1967; Nam & Saito, 1995; Gil-Rodriguez & Haroun, 1992
<i>L. iridescens</i> Wynne <i>et</i> Ballantine	Wynne & Ballantine, 1991
<i>L. kangiaewonii</i> Nam <i>et</i> Sohn	Nam & Sohn, 1994
<i>L. majuscula</i> (Harvey) Howe	Saito, 1969a; Cribb, 1983; Gil-Rodriguez & Haroun, 1992; Wynne, 1995
<i>L. maris-rubri</i> Nam <i>et</i> Saito	Nam & Saito, 1995
<i>L. nipponica</i> Yamada	Masuda <i>et al.</i> , 1992; Nam <i>et al.</i> , 1991; Saito, 1967
* <i>L. obtusa</i> (Hudson) Lamouroux	Nam <i>et al.</i> , 1994; Saito, 1967, 1982; Gil-Rodriguez & Haroun, 1992
<i>L. papillosa</i> (C. Agardh) Greville	Nam & Saito, 1995; Masuda <i>et al.</i> , 1997c
<i>L. parvipapillata</i> Tseng	Tseng, 1942; Saito, 1969; Wynne, 1995
<i>L. saitoi</i> Perestenko	Masuda & Abe, 1993; Saito, 1967 (as <i>L. obtusa</i>)
<i>L. similis</i> Nam <i>et</i> Saito	Nam & Saito, 1991; Nam & Sohn, 1994; Masuda <i>et al.</i> , 1997c
<i>L. transluida</i> Fujii <i>et</i> Cordeiro-Marino	Fujii & Cordeiro-Marino, 1996
<i>L. tunida</i> Saito <i>et</i> Womersley	Nam & Saito, 1995; Saito & Womersley, 1974
<i>L. undulata</i> Yamada	Cormaci <i>et al.</i> , 1994; Nam & Sohn, 1994; Saito, 1967
<i>L. venusta</i> Yamada	Saito, 1964; Saito, 1967
<i>L. viridis</i> Gil-Rodriguez <i>et</i> Haroun	Gil-Rodriguez & Haroun, 1992
<i>Osmundea crispa</i> (Hollenberg) Nam	Smith & Hollenberg, 1943; Nam <i>et al.</i> , 1994; Saito, 1969b
<i>O. hybrida</i> (de Candolle) Nam	Saito, 1982; Nam & Saito, 1994
# <i>O. osmunda</i> (Gmelin) Nam <i>et</i> Maggs	Nam <i>et al.</i> , 1994; Maggs & Hommersand, 1993
^{oo} <i>O. pelagosae</i> (Schiffner) Ercegovic	Furnari & Serio, 1993b
** <i>O. pinnatifida</i> (Hudson) Stackhouse	Nam <i>et al.</i> , 1994; Furnari & Serio, 1993a; Saito, 1982
<i>O. spectabilis</i> (Postels <i>et</i> Ruprecht) Nam	Nam <i>et al.</i> , 1994; Saito, 1969b
<i>O. truncata</i> (Kützting) Nam <i>et</i> Maggs	Cormaci <i>et al.</i> , 1994; Nam <i>et al.</i> , 1994; Furnari & Serio, 1993a; Maggs & Hommersand, 1993
<i>O. verlaquei</i> Furnari	Cormaci <i>et al.</i> , 1994

^otype of *Laurencia* subg. *Chondrophycus**type of *Laurencia*#type of *Osmundea*^{oo}type of *Laurencia* section *Pelagosae***type of *Laurencia* section *Pinnatifidae* and subg. *Saitoa*

Table 2. Characters and their character states used in the analysis.

Character	Character states
1. Habitat	0, subtidal; 1, low intertidal; 2, mid to high intertidal
2. Adhering to paper	0, yes; 1, no
3. Texture	0, soft; 1, cartilaginous
4. Iridescent	0, absent; 1, present
5. Plant size	0, 1-5 cm; 1, 6-10 cm; 2, ca 15 cm; 3, > 20 cm
6. Axis diameter	0, 1-3 mm; 1, ca 1 mm or less; 2, > 3 mm
7. Branching	0, radial; 1, distichous
8. Axis shape	0, terete; 1, compressed
9. Percurrent axis	0, present; 1, absent
10. Numerous short branchlets	0, absent; 1, present
11. Stolonerous base	0, present; 1, absent
12. Number of pericentral cells	0, four; 1, two
13. Epidermal palisade	0, absent; 1, present
14. Dome shaped epidermal cells	0, absent; 1, slight; 2, conspicuous
15. Epidermal cell secondary pit connections	0, present; 1, absent
16. Epidermal cells radially elongate	0, present; 1, absent
17. Epidermal cell size	0, large (> 40 µm); 1, small (< 30 µm)
18. <i>Corps en cerise</i>	0, absent; 1, one only per cell; 2, one or two per cell
19. Spermatangial pits	0, absent; 1, cup-shaped; 2, pocket
20. Spermatangial development	0, trichoblast; 1, filament
21. Spermatangial axial cell row	0, recognizable; 1, unrecognizable
22. Spermatangial nucleus	0, central; 1, apical
23. Spermatangial cell length	0, 7-10 µm; 1, 10-15 µm; 2, > 15 µm
24. Origin of spermatangial branches (Sp. Br.)	0, trichoblasts; 1, apical epidermal
25. Terminal cell number (Sp. Br.)	0, single; 1, clusters
26. Terminal cell shape (Sp. Br.)	0, ovoid to spherical to elongate; 1, highly elongate
27. Procarp segments (pericentral cell)	0, 5P; 1, 6P; 2, 4P
28. Auxiliary cell timing	0, normal; 1, delayed
29. Protuberant ostiole	0, absent; 1, present
30. Tetrasporangial origin	0, pericentral cells; 1, epidermal cells
31. Tetrasporangial development	0, adaxial; 1, abaxial; 2, lateral
32. Tetrasporangial arrangement	0, parallel; 1, right angle
33. Tetrasporangial position (on pericentral cell, P)	0, P 2-3; 1, P 3-4; 2, P 3-5
34. Tetrasporangial diameter	0, to ca 100 µm; 1, 100-150 µm; 2, > 150 µm; 3, ca 35 µm
35. Additional tetrasporangial pericentral cells	0, absent; 1, present; 2, NA
36. Cover cells	0, longitudinal; 1, horizontal

Table 3. Data matrix. Note: question marks (?) indicate missing data or non-applicable characters.

Taxa	Characters						
	1-5	6-10	11-15	16-20	21-25	26-30	31-36
<i>Chondria</i>	000?3	00000	00000	00000	0??00	000?0	0???10
<i>Osmundea</i>							
<i>O. osmunda</i>	00102	21100	12001	?1021	1?011	00?01	203?20
<i>O. crispa</i>	1?101	001?0	020?1	11021	1?111	00?01	203020
<i>O. hybrida</i>	10102	11000	12001	00011	1?011	01?01	203120
<i>O. pelagosae</i>	00102	01100	12000	00021	111?0	1??01	203020
<i>O. pinnatifida</i>	20103	01100	02001	?1021	1?011	?0001	203?20
<i>O. spectabilis</i>	10113	21100	12010	?0021	11011	00001	203020
<i>O. truncata</i>	1?101	11100	12000	00011	1?011	0??11	20302?
<i>O. verlaquei</i>	2?101	01100	12000	01?2?	1?010	1???1	20312?
<i>Laurencia</i>							
<i>L. obtusa</i>	10012	100?0	01010	10110	01000	00010	101?01
<i>L. composita</i>	2?001	10001	01000	11110	01000	0??00	10110?
<i>L. crustiformans</i>	1?110	10000	1?000	111??	?????	???00	?1?3??
<i>L. majuscula</i>	00002	00000	01010	10210	0?300	???00	10?0??
<i>L. nipponica</i>	10003	00000	01010	10110	00000	00?00	101101
<i>L. saitoi</i>	20002	00001	11010	11210	01000	0?200	10?101
<i>L. similis</i>	01102	00001	11000	11110	01000	0?200	111101
<i>L. venusta</i>	101?1	10000	01010	10?10	01000	00?10	10100?
<i>L. viridis</i>	11102	00000	01000	11110	?????	0?300	10?20?
<i>Chondrophycus</i>							
<i>C. cartilaginea</i>	?1101	00111	12021	00010	01100	00110	112211
<i>C. capituliformis</i>	101?2	00000	02101	?0?1?	?01?0	02?10	?1011?
<i>C. gemmifera</i>	01102	00001	12020	10010	01100	00?10	110&1011
<i>C. intermedia</i>	111?2	00000	02101	01?10	01100	02?10	11001?
<i>C. iridescens</i>	?1110	00011	02020	110??	?????	???00	11001?
<i>C. kangjaewonii</i>	00102	21100	12011	11010	01100	00100	102211
<i>C. maris-rubri</i>	?11?1	0000&11	12001	01???	?1???	?????	110201
<i>C. papillosa</i>	0&1?102	00001	02101	?1010	01000	0??10	11001?
<i>C. parvipapillata</i>	11100	01101	02120	010??	?????	???10	?1011?
<i>C. translucida</i>	10002	10000	12001	?0010	01100	00?10	101111
<i>C. tumida</i>	1???2	00000	12101	01?30	0120?	02?00	11011?
<i>C. undulata</i>	111?0	21110	02001	000??	?????	?0100	112111

Phylogenetic analysis was carried out using PAUP v. 3.1.1 for the Macintosh (Swofford, 1993), and implemented the heuristic search algorithm. The search routine used 100 replications under the random addition option in which only the shortest trees were kept during each replication. The following options were maintained for all analyses: TBR swapping, COLLAPSE and Steepest descent. Character changes were mapped according to the acceleration transformation criterion (ACCTRAN). Thus, where number of steps remains equal, character interpretation favoured the single origin of a character followed by reversal, rather than preferring multiple origins for a character (DELTRAN). Alternative phylogenetic hypotheses were reconstructed and evaluated in MacClade V. 3.01 (Maddison & Maddison, 1992).

RESULTS AND DISCUSSION

Intergeneric relationships of *Osmundea*, *Laurencia* and *Chondrophyucus*

The heuristic searches produced 12 most parsimonious (MP) cladograms with treelength (TL) of 148 and a consistency index (CI) of 0.37 (Figs 1-2). In the majority rule consensus tree (Fig. 2), all species except *L. translucida* were placed in one of three major clades consisting of species assignable to *Laurencia* subg. *Laurencia*, *Laurencia* subg. *Chondrophyucus* and *Osmundea*. In all of the MP cladograms *Laurencia* subg. *Laurencia* was the sister group to the *Laurencia* subg. *Chondrophyucus* and *Osmundea* assemblage. Inclusion of *L. translucida* as part of the subg. *Chondrophyucus* clade required a TL of 149. An additional step (TL=150) was required to include *L. translucida* in either *Osmundea* or subg. *Laurencia*.

Alternative arrangements of the primary lineages were evaluated. When *Osmundea* was placed as the outgroup to the remainder of the complex, TL was two steps longer than the MP cladograms. Alternatively, when subg. *Chondrophyucus* was placed as the outgroup, TL was four steps longer than MP trees. A primary character supporting the hypothesis that subg. *Laurencia* is plesiomorphic within the overall assemblage is the number of pericentral cells. In subg. *Laurencia* there are four pericentral cells in vegetative axes whereas in the remainder of the assemblage there are only two. It is of interest that in *Osmundea* and subg. *Chondrophyucus* fertile axes (procarpic and/or tetrasporic axes) have a larger number of pericentral cells, consistent with the argument that their ancestors had additional pericentral cells in vegetative axes, and that these were lost in the ancestor to *Osmundea* and subg. *Chondrophyucus*.

These cladistic analyses support hypotheses of monophyly for: 1) *Osmundea*, 2) subg. *Laurencia*, 3) subg. *Chondrophyucus* (with possible exception of *L. translucida*), and 4) the *Osmundea* plus subg. *Chondrophyucus* clade. Subg. *Chondrophyucus* is more closely related to *Osmundea* than it is to subg. *Laurencia*. Accordingly, either one or three genera should be distinguished for the entire complex. Given the recent generic characterization of *Osmundea* by Nam *et al.* (1994), the nature of the features that characterize the three lineages (Table 3), and the number of species in the entire complex, we conclude that three genera are appropriate for the assemblage. *L. translucida* is included in subg. *Chondrophyucus* based on the number of pericentral cells in vegetative axes and the reproductive morphology associated with spermatangial development. Accordingly, subg. *Chondrophyucus* is raised to generic rank and distinguished from *Laurencia* *sensu stricto*. A Latin diagnosis and designation of type species was previously provided by Saito (1967). The transfers to *Chondrophyucus* are presented below.

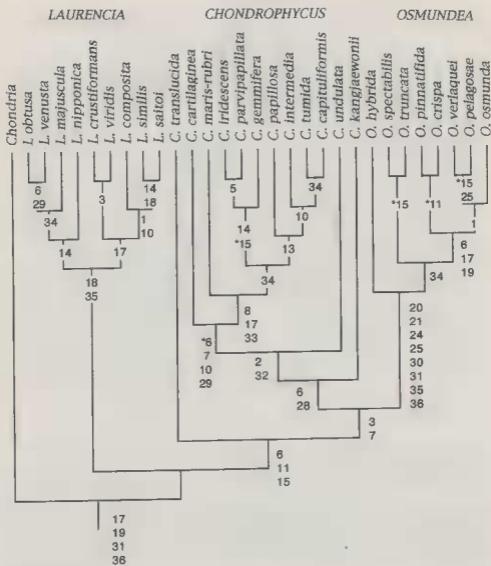


Fig. 1. One of 12 most parsimonious (MP) cladograms (TL = 148; CI = 0.37) from heuristic analysis. Note: variation in MP cladograms occurs only within *Laurencia* and within the crown assemblage of *Chondrophyucus*. Numbers below nodes indicate characters that are synapomorphies for that clade. Apomorphies for terminal clades not indicated; all taxa except *L. obtusa*, *L. viridis*, *C. intermedia* have apomorphies. * indicates character reversals. Without additional outgroups polarities of root characters cannot be determined; thus character changes for characters 17, 19, 31 and 36 may be occurring within either *Chondria* or the *Laurencia* complex.

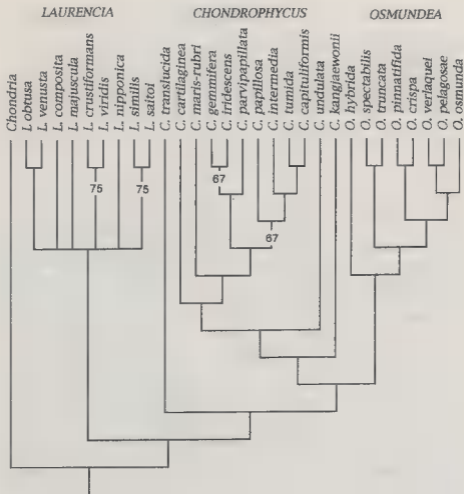


Fig. 2. Majority rule consensus tree based on 12 most parsimonious (MP) cladograms. Numbers on tree show percentage of the MP trees with that topology; unless indicated otherwise, values are 100%. Polytomies indicate that less than 50% of MP cladograms have a single arrangement for the clade. Note the uncertainty within *Laurencia*.

Corynecladia Agardh (1876), with the lectotype species *C. clavata* (Sonder) Agardh [Basonym: *Laurencia clavata* Sonder (1853)], provides a generic name that potentially has priority over *Chondrophyucus* Saito. *L. clavata* was originally described from Australia (Sonder 1853). In the Saito & Womersley (1974) monograph of *Laurencia* from southern Australia *L. clavata* was assigned to section *Laurencia* of subgenus *Laurencia* based on vegetative and reproductive morphology. Hence *Corynecladia* need not be considered further as an older name for *Chondrophyucus*.

The morphological distinctions that form the basis for the primary cladogram topology in Figs 1-2 have been discussed by several recent authors (e.g., Nam *et al.*, 1994; Furnari & Serio, 1995; Fujii & Cordeiro-Marino, 1996). Furnari & Serio (1995) and Fujii & Cordeiro-Marino (1996) argue against a further generic rank segregation from *Laurencia* (i.e. separation of *Chondrophyucus*) because of the occurrence of apparent intermediate species. All of these apparently problematic taxa can be assigned with the possible exception of *L. translucida*. However, based on the presence of two pericentral cells in vegetative axes and the presence of the trichoblast type of spermatangial development (Fujii & Cordeiro-Marino, 1996), this species is also assigned here to *Chondrophyucus*. Within *Chondrophyucus*, *C. translucida* comb. nov. merits segregation from other species at sectional or subgeneric ranks.

The three genera, *Laurencia*, *Chondrophyucus* and *Osmundea*, can be easily distinguished from each other based on a combination of vegetative and reproductive criteria (Table 4). *Laurencia* (Fig. 1) has four pericentral cells in vegetative axes, secondary pit connections between superficial cortical cells, spermatangial development of the trichoblast type and tetrasporangia originating from pericentral cells. A *corps en cerise* is also diagnostic. To date, this structure has only been observed in species that are unequivocally members of *Laurencia* as defined here. This feature can only be observed in living cells. Because *L. venusta* has been described based on only formalin preserved material, the occurrence of a *corps en cerise* cannot be documented in this species. Masuda *et al.* (1997c) only recently characterized the *corps en cerise* in *L. similis*.

Table 4. Summary of diagnostic features for *Laurencia*, *Chondrophyucus* and *Osmundea*. Note: character number in parentheses. Exceptions to character states listed below.

Character	<i>Laurencia</i>	<i>Chondrophyucus</i>	<i>Osmundea</i>
Branching (7)	radial	radial and distichous	distichous ¹
Number of pericentral cells (12)	four	two	two
Epidermal secondary pit connections (15)	present	absent	absent or present
<i>Corps en cerise</i> (18)	present	absent	absent
Spermatangial pits (19)	cup	cup	cup and pocket
Spermatangial development (20)	trichoblast	trichoblast	filament
Tetrasporangial origin (30)	pericentral cells	pericentral cells	epidermal cells
Tetrasporangial arrangement (32)	mostly parallel ²	mostly right-angle ³	parallel
Additional tetrasporangial pericentral cells (35)	absent	present	NA
Tetrasporangial cover cells (36)	horizontal	horizontal	longitudinal

¹radial branching rare, e.g., *O. crispata*

²rarely right-angled, e.g., *L. similis*, *L. crustiformans*

³rarely parallel, e.g., *C. kangjaewonii*

Diagnostic features for *Osmundea* (Fig. 1) include the following: two pericentral cells in vegetative axes, spermatangial development of the filament type, tetrasporangial origin from epidermal cells and the parallel arrangement of tetrasporangia. Other features that occur in most species include distichous branching (except *O. crispa*), multiple enlarged cells at the end of spermatangial filaments (*O. verlaquei*, *O. pelagosae* are exceptions), and spermatangia 7-10 μm long (only *O. pelagosae* has larger spermatangia). Spermatangia in pocket shaped depressions (Nam *et al.*, 1994) are also found only in *Osmundea*, but not all species show this feature.

Chondrophyucus (Fig. 1) also has a suite of features that distinguishes it from *Osmundea* and *Laurencia*. These include: two pericentral cells in vegetative axes, spermatangial development of the trichoblast type, and tetrasporangial development from pericentral cells (Saito, 1967; Nam & Sohn, 1994). The absence of secondary pit connections between adjacent cortical cells also characterizes most of the species considered here (*C. iridescens* comb. nov., *C. gemmifera* comb. nov., *C. parvipapillata* comb. nov. are exceptions). This is relevant to the extent that when epidermal secondary pit connections are absent, then the taxon cannot be attributed to *Laurencia*. The spermatangia of all *Chondrophyucus* species described to date are $>10 \mu\text{m}$ long. Outside of *Chondrophyucus*, the only species to have the same large spermatangia is *O. pelagosae*. Unfortunately, spermatangial lengths are unavailable for many species in all three genera. Nam & Sohn (1994) described a delay in auxiliary cell formation after presumed fertilization in *C. undulata* comb. nov., *C. kangjaewonii* comb. nov. and *C. cartilaginea* comb. nov. This feature is currently unknown in either *Osmundea* or *Laurencia*, and may be diagnostic for *Chondrophyucus*.

New combinations in *Chondrophyucus*

Chondrophyucus (Tokida *et Saito in Saito*) stat. nov.

Synonym: *Laurencia* subgenus *Chondrophyucus* Tokida *et Saito in Saito* (1967). *Memoirs of the Faculty of Fisheries Hokkaido University*, Vol. 15 (1), p. 72.

Type species: *Chondrophyucus cartilaginea* (Yamada) comb. nov.

Basionym: *Laurencia cartilaginea* Yamada (1931), *University of California Publications in Botany*, Vol. 16, p. 230, pl. 19, fig. a, text-figure O.

Diagnosis: Thalli with typical rhodomelacean morphology with apical pits and two pericentral cells in vegetative axes. Secondary pit connections between epidermal cells mostly absent, and all species without *corps en verise*. Thalli with cup-shaped spermatangial pits and spermatangial development associated with trichoblasts. Tetrasporangia developing from pericentral cells and with fertile branches producing additional fertile pericentral cells; tetrasporangia typically arranged in right angle pattern.

Chondrophyucus capituliformis (Yamada) comb. nov.

Basionym: *Laurencia capituliformis* Yamada (1931), *University of California Publications in Botany* 16: 217, pl. 14.

Chondrophyucus gemmifera (Harvey) comb. nov.

Basionym: *Laurencia gemmifera* Harvey (1853), *Smithsonian Contributions to Knowledge* 5 (5): 73-74, pl. XVIII, B.

Chondrophycus intermedia (Yamada) comb. nov.

Basionym: *Laurencia intermedia* Yamada (1931), *University of California Publications in Botany* 16: 191, pl. 1, fig. C, pl. 2.

Chondrophycus iridescens (Wynne et Ballantine) comb. nov.

Basionym: *Laurencia iridescens* Wynne & Ballantine (1991), *Phycologia* 30: 395-397, figs 1-11.

Chondrophycus kangjaewonii (Nam et Sohn) comb. nov.

Basionym: *Laurencia kangjaewonii* Nam et Sohn (1994), *Phycologia* 33: 397-398, figs 1-21.

Chondrophycus maris-rubri (Nam et Saito) comb. nov.

Basionym: *Laurencia maris-rubri* Nam et Saito (1995), *Phycologia* 34: 162, figs 22-29.

Chondrophycus papillosa (C. Agardh) comb. nov.

Basionym: *Chondria papillosa* C. Agardh (1822), *Species algarum* . . . Vol. 1, pt 2, p. 344.

Chondrophycus parvipapillata (Tseng) comb. nov.

Basionym: *Laurencia parvipapillata* Tseng (1943), *Papers of the Michigan Academy of Science Arts and Letters* 28: 204-205, pl. IV.

Chondrophycus translucida (Fujii et Cordeiro-Marino) comb. nov.

Basionym: *Laurencia translucida* Fujii et Cordeiro-Marino (1996), *Phycologia* 35: 542-543, figs 1-25.

Chondrophycus tumida (Saito et Womersley) comb. nov.

Basionym: *Laurencia tumida* Saito et Womersley (1974), *Australian Journal of Botany* 22: 846-847, figs 5E, F, 26, 27.

Chondrophycus undulata (Yamada) comb. nov.

Basionym: *Laurencia undulata* Yamada (1931), *University of California Publications in Botany* 16: 243, pl. 29, fig. a, text-figure T.

Hypotheses for infrageneric relationships within *Laurencia*, *Chondrophycus* and *Osmundea*

Relationships within *Laurencia* were poorly defined by this analysis. The majority rule consensus tree (Fig. 2) showed reasonable support for three pairs of species (*L. obtusa* and *L. venusta*; *L. crustiformans* and *L. viridis*; *L. satoi* and *L. similis*). In one of the 12 fully resolved cladograms (Fig. 1) epidermal cell size characterizes two clusters of species (*L. nipponica*, *L. majuscula*, *L. venusta* and *L. obtusa* with large cells, and *L. crustiformans*, *L. similis*, *L. viridis*, *L. satoi* and *L. composita* with small cells). The large celled species also have epidermal cells with a slight dome shape, although this also occurs in *L. satoi*. Characterization of relationships within *Laurencia* will require a greater sampling of species, and a more specialized character list for these species.

Although *Chondrophycus* forms a monophyletic assemblage (apart from the problematic *Chondrophycus translucida*), relationships within the genus are reasonably well defined with variation among MP cladograms present in only two of the crown groups (Fig. 2). *C. kangjaewonii* is an outlier in *Chondrophycus* where it forms the apparent sister group. When they described *C. kangjaewonii* Nam & Sohn (1994) suggested that this species was intermediate between subgenera *Laurencia* and *Chondrophycus*. According to

Figs 1-2, *C. kangjaewonii* is closer to *Osmundea* than *Laurencia*. If an infrageneric classification for *Chondrophycus* is elaborated at the sectional or subgeneric ranks, one of the resulting taxa should be erected for *C. kangjaewonii*. *C. undulata*, *C. cartilaginea* and *C. maris-rubri* form successive sister groups to the remaining clusters of species. The primary character that suggests affinity of *C. undulata* with the main group of *Chondrophycus* species rather than with *C. kangjaewonii* or *C. translucida* is the right-angle tetrasporangial arrangement.

The remaining seven species of *Chondrophycus* (Fig. 1) correspond to what Nam & Saito suggested are a monophyletic assemblage within the complex, and they are characterized by large rather than small or medium sized tetrasporangia. There are two groups of species that also may be natural groups. The first clade includes *C. iridescens*, *C. gemmifera*, and *C. parvipapillata*. This clade is characterized by dome-shaped epidermal cells at apices and the presence of epidermal secondary pit connections. Another clade within *Chondrophycus* includes *C. papillosa*, *C. capituliformis*, *C. intermedia* and *C. tumida*. These species form an epidermal palisade (also in *C. parvipapillata*), and form the carpogonial branch associated with pericentral cell four (unknown in *C. papillosa*) (Nam & Saito, 1995). This latter grouping of species corresponds to what has previously been characterized as Section *Palisadae* (except for *C. papillosa*).

Osmundea was clearly defined as a monophyletic group and it was the most highly supported clade in the analysis (Fig. 1). Relationships within the genus are fully resolved and *O. hybrida* appears to be the sister group to the remaining species. The latter assemblage is characterized by the occurrence of small tetrasporangia (except *O. verlaquei*). It is divided into two clades. The *O. spectabilis* and *O. truncata* clade is characterized by epidermal secondary pit connections. This appears to be independently derived relative to the occurrence of this feature in *O. verlaquei* and *O. pelagosae*, although it would be of interest if other features could be found to join these four species.

The *O. pinatifida*, *O. crispa*, *O. osmunda*, *O. verlaquei* and *O. pelagosae* lineage forms a well characterized assemblage based on the occurrence of medium to large diameter vegetative axes, small epidermal cells (except *O. pelagosae*) and pocket-shaped spermatangial pits. The latter character was emphasized in the morphological analyses of Nam *et al.* (1994). The *O. verlaquei* and *O. pelagosae* clade seems to be well defined based on the highly elongate and single terminal cells on spermatangial branches and the occurrence of secondary pit connections between epidermal cells (also in the *O. spectabilis* and *O. truncata* lineage).

Additional morphological characters

One of the problems in a morphologically based phylogenetic analysis is the determination of characters and the designation of character states for individual taxa. This is especially the case for studies such as this which are primarily based on character interpretations in the literature and the variable use of descriptive terms. Our study points to several other characters which may be of taxonomic significance in the complex but were not utilized in our character matrix. These include colour, occurrence of cortical rhizoidal filaments and occurrence of lenticular thickenings.

Colour was alluded to as a systematic character by Gil-Rodríguez & Haroun (1992), who compared *L. viridis* with other "green" species in the complex. We found that the attribution of colour involved the utilization of too many character states (*i.e.*, green, red, brown, pink, purple and mixtures of these) to be useful. It may be that when actual

pigments that provide the basis for these colour differences have been resolved, or when colour differences are applied to particular complexes of species, that they may be taxonomically useful.

Rhizoidal cortication has been described for *L. nipponica* (Nam *et al.*, 1991) and has been described for at least one species in each genus (e.g., *C. kangjaewonii*, Nam & Sohn, 1994; *O. hybrida*, Nam & Saito, 1994); however, this character has not been determined for about half the species included here, and thus was omitted from the final analysis.

The presence or absence of lenticular thickenings on medullary cells (e.g., Masuda *et al.*, 1996) is an important character for species discrimination. In preliminary cladistic analyses this feature had an extremely low value for consistency index (< 0.1), and it was present or absent in all major lineages apparently at random [It is also variable in *Chondria* (Gordon-Mills & Womersley, 1987)]. Consequently, it was omitted from the final analysis. Future morphological studies of individual genera or species complexes should include this feature.

Other vegetative characters that may be useful include developmental details associated with phyllotaxy (Masuda *et al.*, 1996), occurrence and development of translucent epidermal cells (Fujii *et al.*, 1996), and occurrence of deciduous branchlets (Masuda *et al.*, 1997a). Reproductive characters that are of potential utility include division patterns of post-sporangial cover cells (e.g., *O. spectabilis*, Nam *et al.*, 1994), and further details of carposporophyte development (Nam *et al.*, 1991).

Chemotaxonomy

Extensive investigations of the chemical composition of a range of *Laurencia* spp. have been carried out. These have focused mostly on terpenoids (e.g., Fenical & Norris, 1975; Masuda *et al.*, 1997b); however, a number of other constituents have been analyzed including bromoallenes (Suzuki *et al.*, 1996), acetogenins (Suzuki *et al.*, 1993) and agar composition (Mahasneh, 1994). These studies often have little chemotaxonomic utility because they typically report the presence of a novel compound from a single species, and the absence of the new compound from other taxa is not reported. Chemotaxonomic utilization is further complicated because of the diversity of chemotypes within even single, well defined species (Masuda *et al.*, 1997b). Constraints on applying chemotaxonomic information in *Laurencia* and red algae in general were discussed by Garbary & Gabrielson (1990). The extensive chemotaxonomic observations of Masuda *et al.* (1997b) on *L. nipponica* and Masuda *et al.* (1997d) on *L. snackeyi* (Weber-van Bosse) Masuda provide an excellent foundation for chemotaxonomic evaluation within species complexes in the overall assemblage. Now that concrete hypotheses for relationships have been formulated for the *Laurencia* complex based on morphological criteria, it would be of interest to extend these analyses to sequence studies based on nucleic acids.

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